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AETOSAURS (ARCHOSAURIA: STAGONOLEPIDIDAE) FROM THE UPPER TRIASSIC (REVUELTIAN) SNYDER QUARRY, NEW MEXICO

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Abstract—Two species of aetosaurs are known from the Snyder quarry (NMMNH locality 3845): *Typothorax coccinarum* Cope and *Desmatosuchus chamaensis* Zeigler, Heckert, and Lucas. Both are represented entirely by postcrania, principally osteoderms (scutes), but also by isolated limb bones. Aetosaur fossils at the Snyder quarry are, like most of the vertebrates found there, not articulated. However, clusters of scutes, presumably each from a single carapace, are associated. *Typothorax coccinarum* is an index fossil of the Revueltian land-vertebrate faunachron (lvf) and its presence was expected at the Snyder quarry, as it is known from correlative strata throughout the Chama basin locally and the southwestern U.S.A. regionally. The Snyder quarry is the type locality of *D. chamaensis*, which is considerably less common than *T. coccinarum*, and presently known from only one other locality. Some specimens we tentatively assign to *D. chamaensis* resemble lateral scutes of *Paratypothorax*, but we have not found any paramedian scutes of *Paratypothorax* at the Snyder quarry, so we refrain from identifying them as *Paratypothorax*. Specimens of both *Typothorax* and *Desmatosuchus* from the Snyder quarry yield insight into the anatomy of these taxa. *Desmatosuchus chamaensis* is clearly a species of *Desmatosuchus*, but is also one of the most distinctive aetosaurs known. Both species of aetosaur from the Snyder quarry appear to be anagenetic descendants from more primitive members of the same genus, *D. chamaensis* from *D. haplocerus* (Cope) and *T. coccinarum* from *T. antiquum* Lucas, Heckert, and Hunt.

Keywords: Revueltian, Stagonolepididae, anagenesis, aetosaur, archosaur, *Desmatosuchus*, *Typothorax*

INTRODUCTION

Aetosaurs are an extinct clade of archosaurs known from Upper Triassic strata on every modern continent except Australia and Antarctica (Heckert and Lucas, 2000). Aetosaur fossils, principally osteoderms (scutes), are relatively common fossils in the Chinle Group in the southwestern U.S.A. (e.g., Long and Ballew, 1985; Long and Murry, 1995; Heckert and Lucas, 1999, 2000). Indeed, aetosaur scutes are often diagnostic to the genus-level, and isolated dorsal or lateral scutes are the type specimens of many aetosaur species, including *Stagonolepis robertsoni* Agassiz, *Desmatosuchus haplocerus* (Cope), *D. chamaensis* Zeigler, Heckert, and Lucas, *Paratypothorax andressorum* Long and Ballew, and *Redondasuchus reseri* Hunt and Lucas (Heckert and Lucas, 2000, 2002a). In this paper we describe the aetosaur fossils from the Snyder quarry (NMMNH locality 3845) in north-central New Mexico and comment on their biochronological and evolutionary significance. NMMNH refers to the New Mexico Museum of Natural History and Science, Albuquerque.

STRATIGRAPHY AND AGE

All of the specimens described here come from the main bonebed at the Snyder quarry. This quarry is stratigraphically high in the Painted Desert Member of the Petrified Forest Formation, approximately 30 m below the Rock Point Formation (Fig. 1). The Painted Desert Member here and across the Colorado Plateau is of Revueltian (Norian) age (Lucas and Hunt, 1993; Lucas, 1998; Lucas et al., 2003). Indeed, *Typothorax coccinarum* is an index taxon of the Revueltian, so its presence at the Snyder quarry helps determine the quarry's age. The occurrence of the phytosaur *Pseudopalatus* at the Snyder quarry (e.g., Zeigler et al., 2002b, 2003a,b) independently corroborates this age assignment, as *Pseudopalatus* is also an index taxon of the Revueltian lvf. The stratigraphic position and age of the quarry are interesting as it is the stratigraphically highest occurrence of *Typothorax* in the Painted Desert Member, although Kirby's (1993) Owl Rock Formation fauna includes *Typothorax* and is stratigraphically above the Petrified Forest Formation. The Snyder quarry is the stratigraphically highest (and therefore youngest) occurrence of *Desmatosuchus*, and it is important to note

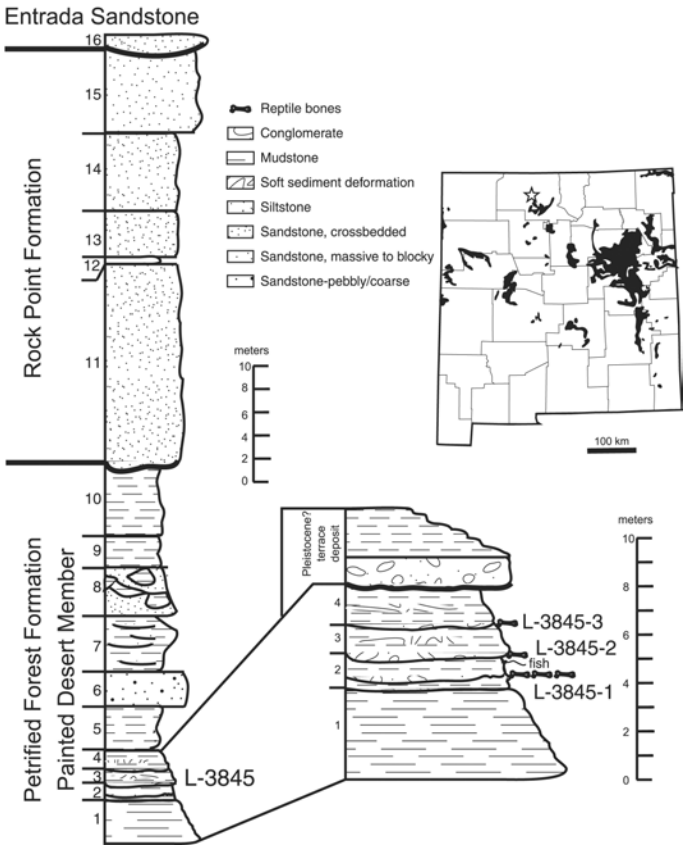

FIGURE 1. Index map showing location of the Snyder quarry site in north-central New Mexico, distribution of Triassic outcrops (from Heckert et al., 2000), and stratigraphic section at the quarry.

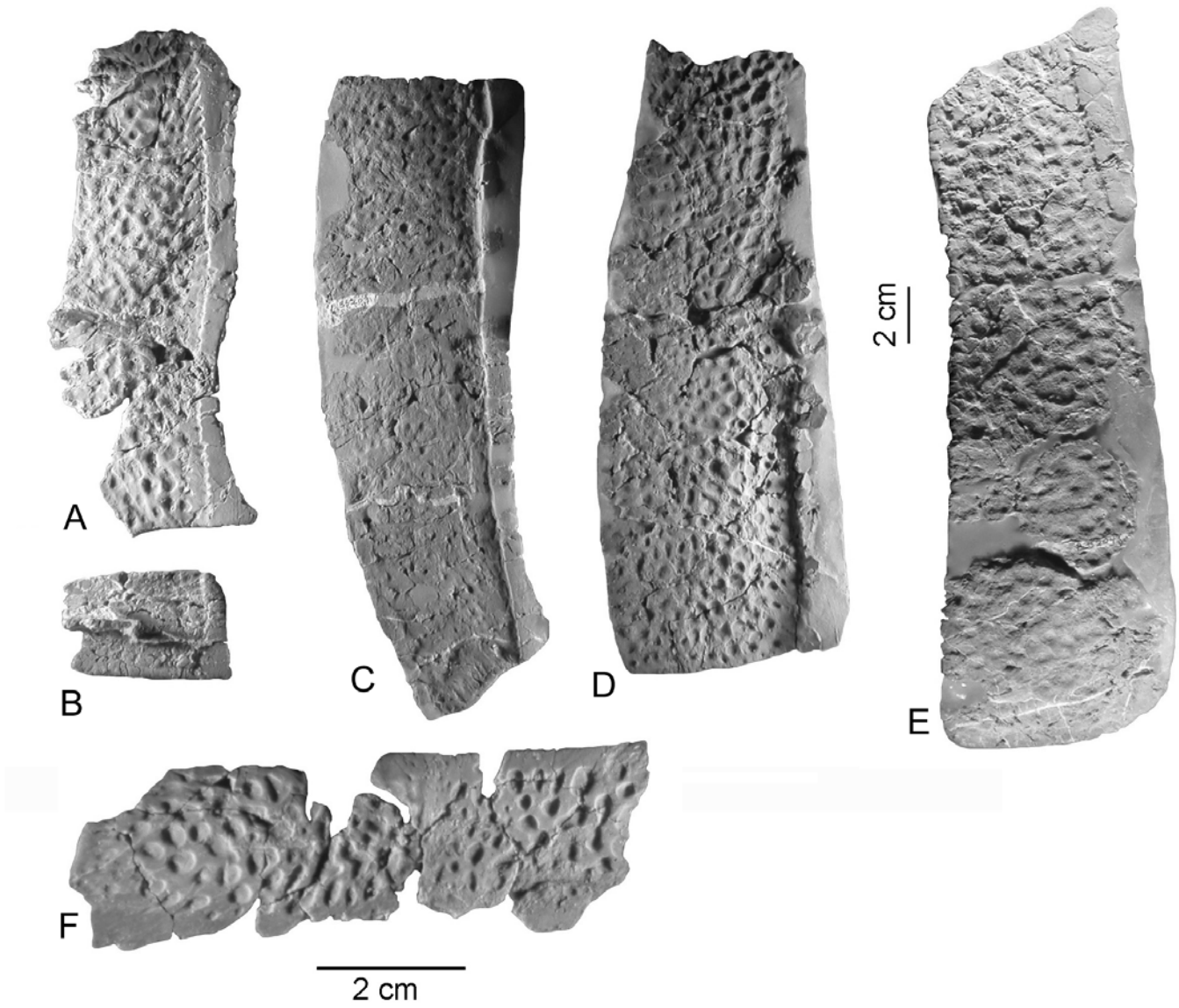

FIGURE 2. Dorsal paramedian (A, C-F) and ventral (B) scutes of *Typothorax coccinarum* from the Snyder quarry. All in external view. **A**, NMMNH P-35205; **B**, NMMNH P-33672; **C**, NMMNH P-35203; **D**, NMMNH P-35990; **E**, NMMNH P-35204; **F**, NMMNH P-37301.

that the entirely Revueltian *D. chamaensis* appears to be an anagenetic descendant of the primarily Adamanian (late Carnian) *D. haplocerus*.

SYSTEMATIC PALEONTOLOGY AND DESCRIPTION

Order Archosauria
Family Stagonolepididae
Genus *Typothorax*
Typothorax coccinarum Cope
(Figures 2-5)

The majority of the identifiable *Typothorax* fossils from the Snyder quarry are isolated osteoderms. *Typothorax* has extremely diagnostic dorsal paramedian and lateral osteoderms (Long and Ballew, 1985; Long and Murry, 1995; Heckert and Lucas, 2000, 2002a; Lucas et al., 2002; Martz, 2002). The paramedian scutes, especially those in the dorsal (thoracic) portion of the carapace, are particularly broad (W:L > 3:1) with prominent ventral keels, as well as a prominent anterior bar and a dorsal ornamentation consisting of a random array of irregular pits but little, if any, dorsal boss. Together, these features are unique to *Typothorax*, and the very broad dorsal paramedian scutes with these characteristics are diagnostic of *T. coccinarum*. The other species of *Typothorax*, *T. antiquum*, has much less broad scutes (Lucas et al., 2002). Similarly, *Typothorax* lateral scutes are distinctive, with a "fold" into a thin dorsal flange and acutely angled lateral flange, with the keel or ridge along the fold enlarged posteriorly into a small horn or spike.

The dorsal paramedian scutes, especially, are readily identifiable on outcrop. To date, we have identified three clusters of *Typothorax* scutes from the Snyder quarry that may pertain to discrete individuals. A jacket containing one of these clusters is currently under preparation at the NMMNH. Based on these clusters, we believe that there are at least two, and perhaps three, adult specimens of *T. coccinarum* represented at the Snyder quarry. A small paramedian scute (described below) indicates the presence of a juvenile as well. These and several other, completely prepared, scutes of *T. coccinarum* well represent the sample from the Snyder quarry, and many of these are illustrated in Figures 2-3.

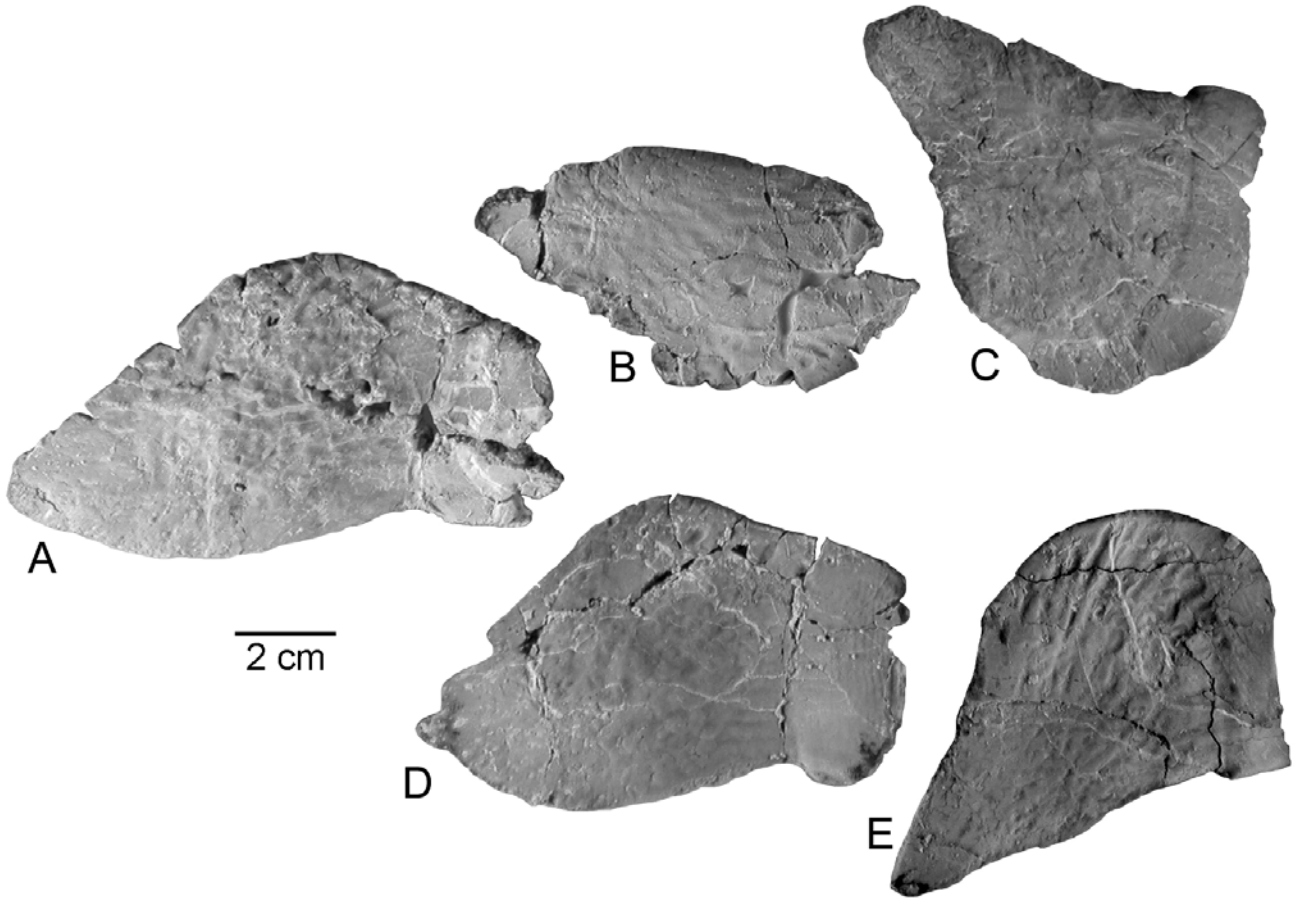

FIGURE 3. Lateral scutes of *Typothorax coccinarum* from the Snyder quarry. All in ventral view. **A**, NMMNH P-39519; **B**, NMMNH P-39518; **C**, NMMNH P-33661; **D**, NMMNH P-35353; **E**, NMMNH P-35352.

There are no cranial fossils of aetosaurs from the Snyder quarry. Presently, we have identified few bones from the Snyder quarry, aside from osteoderms, that pertain to *Typothorax*. Many of the centra and vertebrae recovered from the Snyder quarry probably pertain to aetosaurs, but most of these are not diagnostic below the level of family, and none are described here. The appendicular elements of *Typothorax* we have identified from the Snyder quarry include an incomplete femur (Figs. 4A,5A), an astragalus (Figs. 4C,5C), and a humerus (Fig. 4B,5B) we identify as aff. *Typothorax*. Long and Murry (1995) illustrated astragali of both *Typothorax coccinarum* and *Desmatosuchus haplocerus*, and Lucas et al. (2002) illustrated the left astragalus and calcaneum of *T. antiquum*. In the following paragraphs we briefly describe some of the most diagnostic *Typothorax coccinarum* fossils from the Snyder quarry.

Paramedian scutes

Most of the catalogued fossils of *Typothorax* from the Snyder quarry are paramedian scutes (8) and lateral scutes (6). Of the former, NMMNH P-35203 (Fig. 2C) is a right dorsal paramedian from the anterior dorsal series. This scute possesses several key characteristics that yield insight into not only basic scute morphology but also the shape of the carapace. This scute was probably from near the shoulder

TABLE 1. Measurements of dorsal paramedian scutes of *Typothorax coccinarum* from the Snyder quarry.All measurements in mm. Length AB = length anterior bar, W Med-DB = width from medial edge to center of dorsal boss, W DB-Lat = width from center of dorsal boss to lateral, margin, AP = as preserved, R = right, L = left, ant = anterior dorsal/cervical, post = posterior dorsal/caudal.

Specimen	Width	Length	Length AB	W Med-DB	W. DB-Lat	Position
P-33689	211	70 (boss) 73 (medial)	8-15	81	117	R post
P-35203	243	73	9-16	N/A	N/A	R ant
P-35204	281	85	12+AP	120	180	L post
P-35205	191AP	67	8-19	85AP	102AP	L post
P-35990	230+AP	92AP	5-17AP	N/A	N/A	R ant
P-37301	81	25	3-5AP	31	52	R mid?
P-39182	222AP	86AP	7-11	88	135AP	R post
P-39735	183	79	5-26	67	102	R post

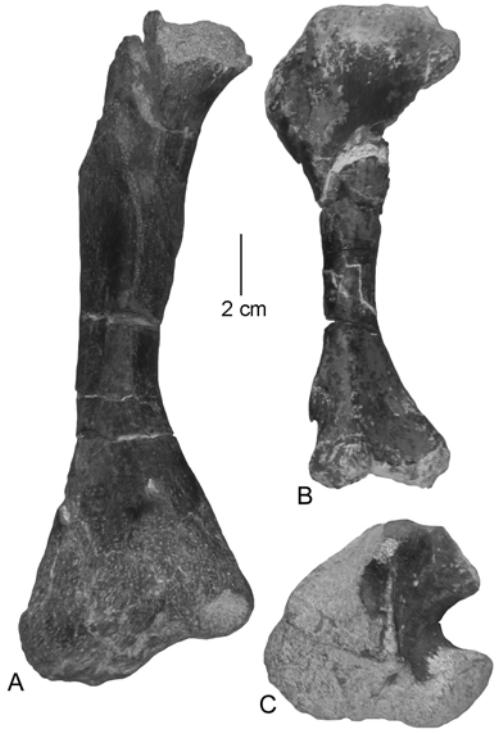

FIGURE 4. Appendicular elements of *Typothorax coccinarum* (A,C) and aff. *Typothorax* (B) from the Snyder quarry. **A**, incomplete femur (NMMNH P-35382) in anterior view; **B**, left humerus (NMMNH P-36070) in lateral view; **C**, left astragalus (NMMNH P33934) in dorsal view.

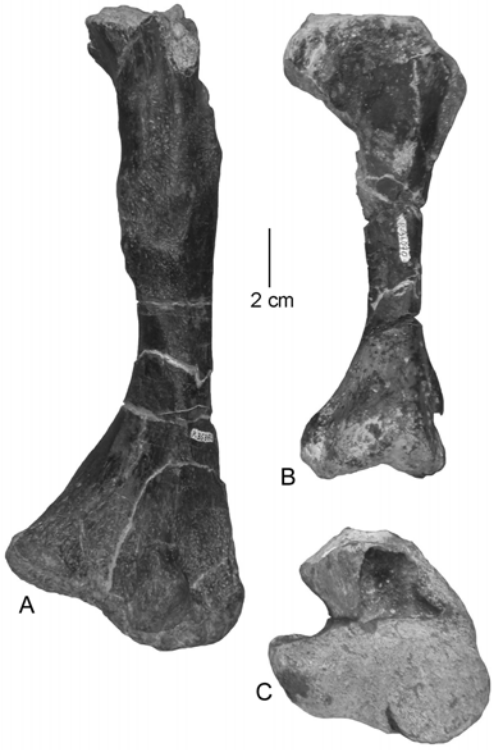

FIGURE 5. Appendicular elements of *Typothorax coccinarum* (A,C) and aff. *Typothorax* (B) from the Snyder quarry. **A**, incomplete femur (NMMNH P-35382) in posterior view; **B**, left humerus (NMMNH P-36070) in medial view; **C**, left astragalus (NMMNH P33934) in ventral view.

region, as the lateral margin is flat for articulation with the corresponding left dorsal paramedian along the midline. As is typical of anterior dorsal paramedian scutes of *Typothorax*, there is no discernable boss. The most striking anatomical feature, however, is the lateral margin. The anterior bar terminates almost 20 mm lateral to the extreme lateral edge of the scute. The lateral margin thus flares posteriorly and presumably would overlap a significantly wider scute posterior to it. Additionally, the ventral keel is faintest medially and stronger laterally.

A similar left dorsal paramedian scute (NMMNH P-35990) also lacks a boss and otherwise has the same general shape. However, its lateral margin is not preserved (Fig. 2D). As in P-35203, the ventral keel is stronger laterally than medially. Presumably both of these scutes are anterior dorsal paramedian scutes, and each is widening posteriorly to create the wide-bodied carapace that typifies *Typothorax coccinarum*.

In contrast, NMMNH P-35204 (Fig. 2E) is a much more posterior dorsal paramedian scute, probably from the anterior caudal series. This scute is strongly arched, and much of the dorsal surface is oriented more dorso-laterally than dorsally. A small, triangular, ridge-like boss is present along the posterior margin of the scute, just medial and posterior to its center. This scute clearly represents the transition from the wider portion of the carapace to the more narrow caudal region. Many aetosaurs retain a wide carapace immediately posterior to the pelvis, so this is probably one of the last wide caudal paramedian scutes.

A somewhat fragmentary left dorsal paramedian scute (NMMNH P-35205, Fig. 2A) is also probably from the caudal region. The lateral margin is not well preserved, but the two lateral-most projections probably represent the lateral margin of the scute. The boss is well developed, and the pitting is similarly strong. The boss contacts the posterior margin of the scute. There is very little evidence of a ventral keel.

Another, right dorsal paramedian scute not illustrated here (NMMNH P-33689) is poorly preserved (and has a ventral[?] scute affixed to its dorsal surface) but also has a tapered postero-medial border, suggesting that it, too, is a caudal scute. The boss is strongly developed and contacts the posterior margin of the scute. The entire scute appears to be strongly arched, but in the antero-posterior plane, not the dorso-ventral plane. It also lacks a ventral keel. A similarly poorly preserved dorsal paramedian scute, NMMNH P-39182, has only the slightest indication of a ventral keel, and we interpret the lack of a ventral keel on the caudal paramedians as a diagnostic feature of *T. coccinarum*.

A single incomplete dorsal paramedian scute (NMMNH P-37301; Fig. 2F) appears to represent a juvenile of *T. coccinarum*. This scute possesses all the diagnostic characteristics of *T. coccinarum* dorsal paramedian scutes: it is much wider than long, has a pronounced ventral keel, a random array of pits on the dorsal surface and an anterior bar. This scute is incomplete, but at least 25 mm long and 81 mm wide. Importantly, the pitting is extremely regular and strongly developed. Similarly, the ventral keel is very prominent. Because this scute has all of the characteristics of *T. coccinarum* but is far smaller than the rest of the sample, we identify it as a juvenile. This implies that the dorsal ornamentation is more evident (pronounced) in juvenile *Typothorax* than in adults, a feature we have documented in other aetosaurs, including *Desmatosuchus* (Heckert and Lucas, 2002b), and *Stagonolepis* (Heckert and Lucas, 2002c). Martz (2002) recently reviewed the ontogeny of *Typothorax*, based in part on the fossils from the nearby Canjilon quarry, and saw relatively few differences in scute morphology between adults and juveniles. He did note that juvenile scutes of *T. coccinarum* generally do not attain the extreme width:length ratio of adults, but the width:length ratio of this scute (3.2:1) lies within that observed by Martz (2002).

Lateral scutes

Typothorax lateral scutes are extremely distinctive (Heckert and Lucas, 2000), and are readily identified in the Snyder quarry sample. Lateral scutes of *Typothorax coccinarum* are acutely folded into two

flanges, a smaller dorsal flange that articulates medially with the corresponding paramedian scute and a larger, ventral flange. The two flanges meet at an acute angle. Along this juncture is a posteriorly recurved spike or horn. Lateral scutes are less heavily ornamented than paramedians. Pitting on the dorsal flange is generally sparse and more or less randomly distributed. The patterning of the ventral flange is more distinct and often consists of a radial array of grooves and ridges. These arcuate ridges and adjoining grooves are concave anteriorly and convex posteriorly. Generally, the dorsal flange is triangular in dorsal view, with an acute anterior edge, a right triangle at the postero-medial corner, and a somewhat less acute angle between the posterior and lateral margins.

The sample available for study from the Snyder quarry consists of two relatively complete right lateral scutes (NMMNH P-33661 and P-39518) and four complete left lateral scutes (NMMNH P-35351, P-35352, P-35353 and P-39519) (Fig. 3). Unlike the dorsal paramedian scutes, there is little size variation among these scutes (Table 2), and all could conceivably pertain to a single adult individual.

A well-preserved right lateral scute (NMMNH P-33661; Fig. 3C) has almost no dorsal flange, and most of the surface of the scute is on the latero-ventral side. Surface ornamentation consists of just a few pits on the minimal dorsal surface and a more fully developed, somewhat radial pattern of pits, ridges, and elongate grooves on the ventral surface. There is a short, relatively blunt spike or boss at the posterior margin. The dorsal and lateral flanges meet at an acute (~60°) angle. NMMNH P-39518 (Fig. 3B) is a similar right lateral scute.

A comparable left lateral scute (NMMNH P-35352; Fig. 3E) is generally similar. The pitting on the ventral surface is better preserved and more clearly shows a subradial pattern of elongate grooves and subdued ridges. Medially, these grooves are concave anteriorly, but straighter (subparallel) closer to the point of the spike from which they originate.

Another morphology of *Typothorax* lateral scutes consists of scutes with a somewhat less acute (~75°) juncture between the lateral flange and a more robust dorsal flange. A typical scute (NMMNH P-35353; Fig. 3D) also has a better-developed gap (sulcus) between the body of the scute and the anterior bar. The boss or spike is much more prominent and bulges laterally, but does not taper to as sharp a point, nor does the boss project as far posteriorly. The ornamentation on both this scute and similar scutes (e.g., NMMNH P-39519: Fig. 3A; NMMNH P-35351) consists of fewer ridges and grooves and more pits. It is not clear from where on the body these scutes originated other than that lefts and rights are readily distinguished.

Ventral scutes

A typical ventral scute (NMMNH P-33672; Fig. 2B) is 63 mm long and 42 mm wide. The scute is essentially rectangular with weakly developed, randomly arrayed pitting. The anterior bar flares out slightly on the presumed lateral side, suggesting that this is a left ventral scute. NMMNH P-33358 and NMMNH P-33359 are similar in size, shape, and ornamentation, except that NMMNH P-33358 may be a right. NMMNH P-33359 is the most symmetrical of these ventral scutes and also has the weakest pitting.

Appendicular elements

The best preserved appendicular element of *T. coccinarum* from the Snyder quarry is a large right astragalus (NMMNH P-33934; Fig. 4C, 5C). This element preserves almost all of the processes and recesses of the astragalus except the most proximal portion of the tibial facet, but is heavily worn along many joint faces. Thus far only Parrish (1986, fig. 28) has illustrated the astragalus of *T. coccinarum*, although the astragalus of *T. antiquum* (Lucas et al., 2002, fig. 9) is similar. The postero-ventral surface is wide (75 mm across), indicating that this was a relatively large (adult) individual. The astragalus of *Typothorax* can be distinguished from that of *Desmatosuchus*, also present in the quarry, by several characteristics. These include the more anterior projection of the tibial facet (evident in part because the broken facet on P-33934 projects farther anteriorly than the corresponding facets of complete *Desmatosuchus* specimens). Both species of *Typothorax* also have a well-developed sulcus on the medial surface of the tibal facet as well as a much more bulbous posterior process, especially laterally, than seen in *Desmatosuchus*. Accordingly, we assign this specimen to *Typothorax coccinarum*.

We have recovered a single incomplete right femur (NMMNH P-35382; Figs. 4A, 5A) from the Snyder quarry we assign to *Typothorax*. The femur of *Typothorax* is readily distinguished from that of *Desmatosuchus* in that it is proportionately shorter and more robust, with much more distinct and robust distal condyles (Long and Murry, 1995). Unfortunately, P-35382 lacks a head, although much of the proximal end remains intact. There is a single elongate ridge or crest on the anterior surface, extending from immediately below the head of the femur almost 3/4 of the way down the shaft. The proximal surface of this ridge is rugose and clearly served as the site of substantial muscle attachments. Lateral to this surface is another rugosity, the greater trochanter, which is somewhat elongate and covers much of the anterodorsal surface of the proximal femur. The fourth trochanter is a massive rugosity on the postero-ventral surface, albeit not as massive as in *Desmatosuchus* (Long and Murry, 1995). Muscle scars trace from the fourth trochanter proximo-dorsally almost to the broken proximal head. As Long and Murry (1995, fig. 110) illustrated, the distal end of the femur is massive and grossly expanded relative to the shaft. Much of this expansion is taken up in the development of a massive lateral condyle and accompanying posterior process, with a large rugose sulcus separating the two. This is the only part of the femur that is more massive than that of *Desmatosuchus*, although the proportionately shorter shaft of the femur indicates that *Typothorax* was probably more graviportal than *Desmatosuchus*.

A single, nearly complete humerus (NMMNH P-35382; Fig. 4B, 5B) from the Snyder quarry, is much more robust than the numerous phytosaur humeri recovered from the site (compare to Zeigler et al., 2003; figs. 4-5). This humerus also has more robust articular end than similarly sized phytosaur humeri. It is not, however, anywhere near as

TABLE 2. Measurements of lateral scutes of *Typothorax coccinarum* from the Snyder quarry.All measurements in mm. AP = as preserved, np = not preserved, R = right, L = left, ant = anterior, post = posterior, D flange = dorsal flange, L flange = lateral flange.

	Length				Width			
Specimen	**D flange**	**L flange**	**Ridge**	**AB**	**ant D flange**	**pos D flange**	**ant L flange**	**pos L flange**
P-33661	73	~ 51	79	12-13	0	31	45	np
P-35352	70	60	82	10-13	6 mac	36	42	78
P-35353	np	50	92	21	16AP	65Ap	45	np
P-39518	51AP	54AP	72L	np	inc	47	inc	np
P-39519	68	42	97	18	16	62	44	73

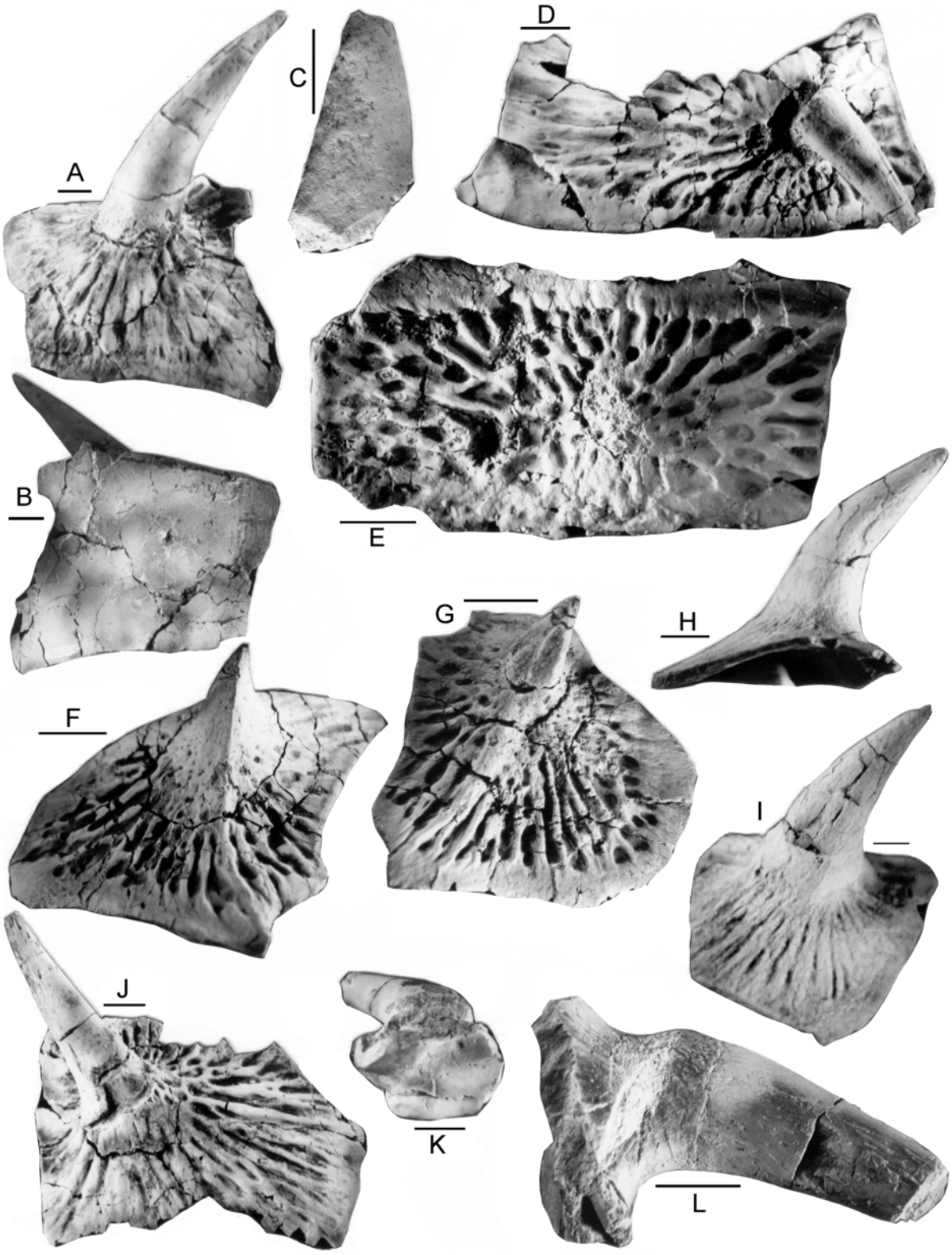

FIGURE 6. The original type and referred material of *Desmatosuchus chamaensis*, all but **C** and **H-I** from the Snyder quarry. **A-B**, Paratype, NMMNH P-32795, right paramedian scute in **A**, dorsal and **B**, ventral views; **C**, Referred specimen, NMMNH P-4894, portions of recurved spike from a cervical scute from the Bull Canyon Formation in lateral view; **D**, Holotype, NMMNH P-32793, right presacral paramedian scute, in dorsal view; **E**, Paratype, NMMNH P-32797, right presacral paramedian scute in dorsal view; **F**, Paratype, NMMNH P-31295, right lateral scute in dorsal view; **G**, Paratype, NMMNH P-32796, left lateral scute in dorsal view; **H-I**, Referred specimen UCM-47725, right paramedian scute from the Bull Canyon Formation, in **H**, lateral and **I**, dorsal views; **J**, Paratype, NMMNH P-33099, left paramedian scute in dorsal view; **K-L**, Paratype, NMMNH P-33100, third lateral cervical horn in **K**, ventral and **L**, dorsal views. Scale bars = 2 cm.

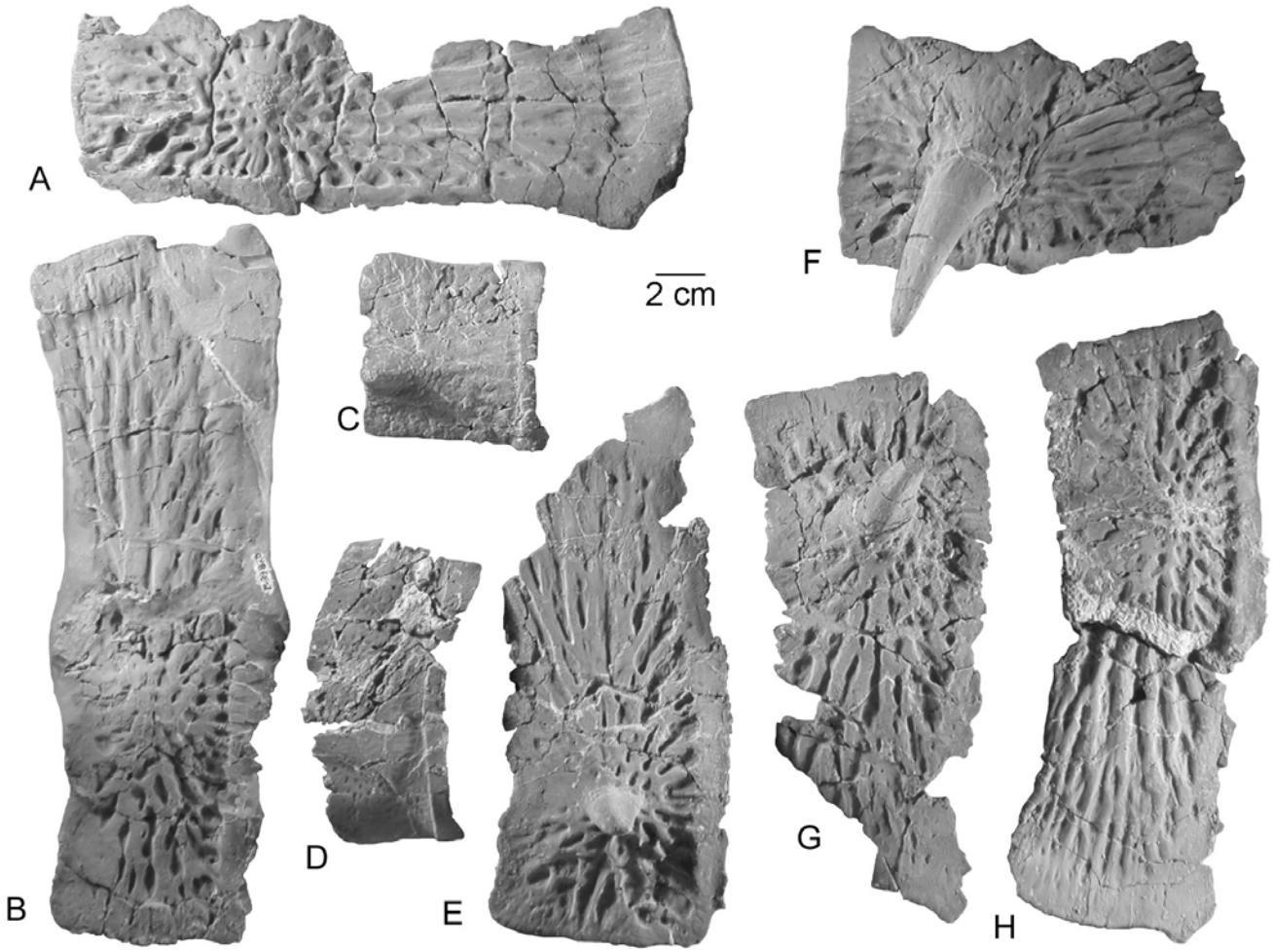

FIGURE 7. Topotype paramedian scutes of *Desmatosuchus chamaensis* from the Snyder quarry, all in dorsal view. **A**, NMMNH P-35807, left; **B**, NMMNH P-33820, left; **C**, NMMNH P-35991, left caudal; **D**, NMMNH P-35206, left; E, NMMNH P-37349, left; **F**, NMMNH P-35459, right; **G**, NMMNH P-35436, right; **H**, NMMNH P-34887, right.

robust as a typical *Desmatosuchus* humerus (Case, 1922; Long and Murry, 1995). Accordingly, we assign it to the Stagonolepididae, aff. *Typothorax*.

Genus *Desmatosuchus*

Desmatosuchus chamaensis Zeigler, Heckert and Lucas

There is little doubt that *D. chamaensis* is one of the most striking aetosaurs known. *Desmatosuchus* is readily distinguished from other aetosaurs by the extremely prominent, posteriorly recurved spikes emanating from its cervical lateral scutes as well as the presence of an anterior lamina, rather than an anterior bar, on the dorsal paramedian and lateral scutes (Long and Ballew, 1985; Heckert and Lucas, 2000, 2002a). *D. chamaensis* is even more distinctive, as it is the only aetosaur with large, recurved spikes on its (presumably cervical?) dorsal paramedian scutes (Zeigler et al., 2002a). The Snyder quarry is the type locality of *D. chamaensis*, and remains the only locality yielding multiple specimens of *D. chamaensis*. Consequently, the specimens we describe here are all either part of the type series (Zeigler et al., 2002a), or else topotypes of *D. chamaensis*. Importantly, some of the appendicular elements from the Snyder quarry are extremely similar to illustrated fossils of *D. haplocerus* (e.g., Case, 1922; Long and Murry, 1995) and dissimilar to *Typothorax* (Hunt et al., 1993; Long and Murry, 1995; Lucas et al., 2002). Accordingly, we assign them to *Desmatosuchus chamaensis* and likewise consider them topotypes.

Zeigler et al. (2002a) described *D. chamaensis* based on the holotype cervical(?) paramedian scute (NMMNH P-32793), three other paramedian scutes (paratypes—NMMNH P-32795, P-32797, and P-33099) and four incomplete lateral scutes (also paratypes—NMMNH P-29045, P-31295, P-32796, P-33100) (Fig. 6). Zeigler et al. (2002a) also referred two other specimens, from the Bull Canyon Formation in east-central New Mexico, to *D. chamaensis* (Fig. 6C, H-I). Since the time of their writing, many other specimens, including some appendicular elements, have been prepared (Table 3; Figs. 7-9). These provide much additional information on the scute morphology of the taxon, as well as data for comparison of the appendicular skeleton to other aetosaurs, particularly *D. haplocerus*. In the following paragraphs we describe much of this new material as well as provide augmented descriptions of the original type series.

Paramedian scutes

The holotype, NMMNH P-32793, is, as described by Zeigler et al. (2002a), a nearly complete right paramedian scute with a small, posteriorly recurved spike and an ornamentation of deep pits and ridges radiating from the spike (Fig. 6D). The posterior edge of the specimen is missing. The scute is 83 mm long and 184 mm wide. The spike is 65 mm long, lacking the tip, broken at the base, and crushed down into the scute body. This spike is smooth in the basal region and bears small foramina and a groove towards the tip. The spike is also sharply re-

curved, and its shape is approximately conical. The ventral side of this scute lacks a ventral keel and possesses a small depression (nutrient foramen?) opposite the dorsal spike. We now interpret this scute as a postero-dorsal or even anterior caudal paramedian, based on the irregular lateral margin with a postero-medial taper.

One of the paratypes, NMMNH P-32795, is a mostly complete presacral paramedian scute from the right side of the body (Fig. 6A-B). It has a long, sharply recurved spike projecting from the right half of the scute body with a strong ridge-and-groove pattern radiating from the spike. The scute is 105 mm long, and 88 mm wide with a spike measuring 110 mm, minus the tip. The spike is smooth in the basal region and bears small foramina towards the tip, together with a thin groove on the dorsal surface of the spike. The spike is sharply recurved, with a conical shape. The posterior margin is broken and missing the medial portion. The ventral surface is smooth, lacks a keel, has a very low degree of curvature, and has a small depression opposite the point where the spike projects from the dorsal side (Fig. 6B). This scute is longer than wide, which is typical of *Desmatosuchus* cervical paramedian scutes, and we interpret it as a cervical paramedian scute, probably from the third or fourth row of scutes.

Another paratype scute, NMMNH P-32797, is a right presacral paramedian that is nearly complete (Fig. 6E). This specimen does not have a recurved spike, but instead has a low boss with a very rugose surface near the center. This boss does not contact the posterior margin of the scute. The ornamentation consists of irregular, shallow pits and long, similarly irregular grooves and ridges radiating from the boss. The scute is 70 mm long and 141 mm wide. The ventral surface lacks either a ventral keel or a depression corresponding to the boss. Because this scute lacks a spike but is relatively narrow (W:L = 2:1), we interpret it as one of the dorsal paramedian scutes immediately anterior to the sacrum. If this is accurate then, like *D. haplocerus*, *D. chamaensis* has a "waist" or constriction anterior to the sacrum.

NMMNH P-33099 is a partial left cervical or presacral paramedian scute possessing a long recurved spike that has been crushed down into the scute body (Fig. 6J). This scute possesses a flat base and has the distinct irregular ridge-and-groove pattern seen on the other paramedian scutes. The scute is 141 mm long and 106 mm wide, with a preserved spike length of 90 mm (the tip is missing). The spike is also smooth in the basal region, with foramina and a faint groove developed near its end. The spike is nearly conical in shape, but has been depressed down against the body of the scute. The ventral surface is smooth, with a small pit corresponding to the dorsal spike. The scute is poorly preserved, but we believe that the enormous (100+ mm long as preserved) spike was recurved posteriorly, making this a left dorsal paramedian. This then results in a typical (except for the spike) *Destmatosuchus* scute: the boss is medial to the center of the scute, and medial margin is straight, and the lateral margin convex.

We interpret NMMNH P-35807 (Fig. 7A) as a left dorsal paramedian scute from the mid-dorsal portion of the carapace. The scute measures 236 mm wide and 76 mm long. This is one of the few *D. chamaensis* scutes that lacks a spike. Instead it looks much like a dorsal paramedian scute of *D. haplocerus*, with a low boss emanating from the dorsal surface of the scute. Importantly, this boss is round, not keeled, oblong, or pointed, and does not contact the posterior margin of the scute. In this way it well-matches diagnoses of *D. haplocerus* paramedian scutes (Long and Ballew, 1985; Long and Murry, 1995; Heckert and Lucas, 2000).

NMMNH P-33820 (Fig. 7B) is similar, albeit much larger (267 mm wide, 75 mm long medially, 93 mm long laterally). This left dorsal paramedian scute is one of the largest *Desmatosuchus* scutes known from the quarry at this time. Otherwise, it is similar to P-35807, albeit better preserved. There is no hint of a ventral keel on this or any other dorsal paramedian from the Snyder quarry. The dorsal patterning consists largely of elongate pits, grooves, and ridges emanating from the

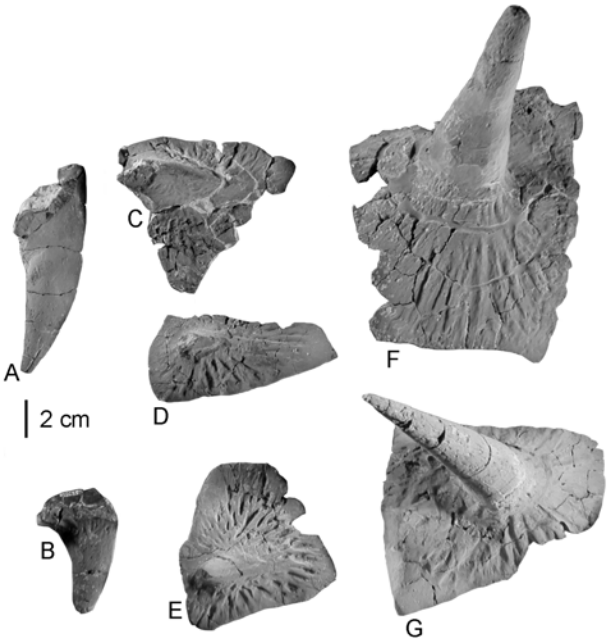

FIGURE 8. Topotype lateral scutes of *Desmatosuchus chamaensis* from the Snyder quarry, all in dorsal view. **A**, NMMNH P-35993, right(?) lateral spike in dorsal(?) view; **B**, NMMNH P-29045, right(?) lateral spike in dorsal(?) view; **C**, NMMNH P-39250, right lateral scute in lateral view; **D**, NMMNH P-39184, caudal(?) lateral(?) spike in lateral(?) view; **E**, NMMNH P-34891, left lateral scute in lateral view; **F**, NMMNH P-36052, left lateral scute in lateral view; **G**, NMMNH P-33101, right(?) lateral spike in lateral(?) view.

TABLE 2. Measurements of scutes of *Desmatosuchus chamaensis* from the Snyder quarry.All measurements in mm. AP = as preserved, RDPM = right dorsal paramedian, LDPM = left dorsal paramedian, LAL = length of anterior lamina, W DB-Med = width from medial edge to dorsal boss, W-DB-Lat = width from lateral edge to dorsal boss, med = medial, lat = lateral.

Specimen	Width	Length	LAL	W DB-Med	W DB-Lat	Spike length	Position
P-32793	199	91	9-14AP	49	127	64AP	RDPM
P-32797	139	68 med 73 med	11-16AP	58	83	N/A	RDPM
P-33099	145	102 AP	np	47	107	87AP	LDPM
P-33820	267	75 med 92 lat	15-22	80	180	N/A	LDPM
P-34887	237	84	15	71	156	~10	RDPM
P-35436	209AP	89AP	10-14AP			52 AP	RDPM
P-35807	236	76 med 83 lat	7-18AP	79	156	N/A	LDPM
P-37349	208AP	89	11-23AP	57	154	26	LDPM

dorsal boss. NMMNH P-33820 and the more fragmentary NMMNH P-37348 (not illustrated) are the two largest dorsal paramedian scutes at the quarry. Indeed, these specimens are wider than any of the reasonably complete *Desmatosuchus haplocerus* scutes in the extensive holdings of the University of California Museum of Paleontology (Berkeley) or Case's (1922) specimen. However, even these large scutes are nowhere near as large as some specimens we have seen from Texas, let alone the enormous specimen under description by Parker (1999). We interpret these scutes as mid-dorsal paramedian scutes because we suspect that many of the relatively long (and less broad) spiked scutes are anterior dorsal paramedian scutes. Similarly, the dorsal boss generally is more pronounced in posterior paramedian scutes, especially in the caudal region (Heckert and Lucas, 2000, 2002b). Therefore, we suspect that *D. chamaensis* may have had spikes on its caudal and posterior dorsal paramedian scutes as well.

For example, NMMNH P-37349 (Fig. 7E) is another left dorsal paramedian scute, approximately 208 mm wide, 89 mm, and generally similar in most respects to the dorsal paramedian scutes described in the preceding paragraphs. However, a rounded spike projects dorsally from the dorsal boss 26 mm above the surface of the scute. Although much of the lateral margin of this scute is damaged, it is intact anteriorly and preserves a distinct postero-medial taper. This indicates that the next most posterior scute was almost surely narrower, and thus P-37349 is probably a proximal caudal left dorsal paramedian. Alternately, *D. chamaensis* may have been "waisted" like *D. haplocerus* (Case, 1922), but we consider this possibility less likely, as the pronounced increase in boss size is usually expressed in the sacral and caudal series of scutes.

NMMNH P-35436 (Fig. 7G) is a similar right dorsal paramedian that is approximately 209 mm wide and 89 mm long. Curiously, the rather large (52 mm long as preserved) spike is slightly recurved anteriorly. Like P-37349, the lateral margin tapers postero-medially, indicating that this is also a caudal paramedian scute, probably one scute position anterior in the column to P-37349.

Likewise, NMMNH P-32793 appears to be a caudal right paramedian scute and is 199 mm wide and 99 mm long. The spike is long (64 mm to the broken end, probably 75 mm or more long), but broken and folded anteriorly over the scute. Like P-35436, the spike appears to be recurved anteriorly, although this is not certain.

NMMNH P-32797 is a left dorsal paramedian scute that most closely resembles a typical *D. haplocerus*. There is a low boss (no spike) just medial to the center of the scute. The scute itself is 139 mm wide and 68 mm long. The medial edge is slightly thickened and, while not well-preserved, may have had the "tongue and groove" articulations seen in cervical dorsal paramedian scutes of *D. haplocerus* (Long and Ballew, 1985; Long and Murry, 1995).

NMMNH P-34887 is a transitional late dorsal right dorsal paramedian scute. The boss is enlarged, but does not yet constitute a spike. The scute is broken, so measurements and shape may not be totally reliable, but it is approximately 237 mm wide and 84 mm long. On the lateral margin there is a complex edge for articulating with the corresponding lateral scute, and the scute appears to taper postero-medially.

Lateral scutes

One of the paratype lateral scutes, NMMNH P-31295, is a nearly complete right lateral scute with a small, recurved spike in the center of the scute body (Fig. 6F). The medial margin has a complex, doubly notched edge. The ornamentation is less distinct than on the dorsal scutes, consisting of shallow ridges and grooves radiating from the spike. The scute body has a greater degree of curvature than any of the paramedian scutes, but is still flatter than those of any other spiked aetosaur. The scute is 75 mm long and 89 mm wide. The spike is 55 mm long, small, and sharply recurved. The surface of the spike is heavily pitted, and the shape is pyramidal due to the presence of a thin ridge along the anterodorsal surface of the spike. The ventral surface of the scute is flat and smooth with only a very faint depression corresponding to the spike. This scute was probably from the anterior portion of the tail, although it does not correspond or articulate with any of the paramedian scutes described from the tail earlier in this paper.

Another of the paratype series, NMMNH P-32796, is a well-preserved left lateral scute (Fig. 6G) that is slightly smaller than NMMNH P-31295. Like NMMNH P-31295, it is slightly angled and possesses a sharp anterior edge on the spike. The scute also has a small, recurved spike and a faintly radial ornamentation of ridges and grooves. The scute body is 79 mm long and 8.3 mm wide. The spike is 45 mm long, although it has been broken in several places. The surface is lightly pitted compared to NMMNH P-31295, but also has the same pyramidal shape due to the anterodorsal ridge. The ventral surface of the scute is very smooth with a faint depression, and the scute body has a wide angle of curvature. Similar, albeit more fragmentary scutes include NMMNH P-35349, P-36502, P-37300, and P-39520.

NMMNH P-36052 is a large right(?) lateral scute (Fig. 8F). Both the anterior and posterior margins are damaged, but there are remnants of an anterior lamina, faintly visible on the right side of the specimen as illustrated in Figure 8F. Elongate grooves and ridges radiate from the base of the spike. The much smaller dorsal flange meets the lateral flange at an approximate right angle. The medial margin is slightly thickened. Dozens of extremely small (1-3 mm diameter) circular pits pock the lateral and posterior margins of the scute. These are unlike the ornamentation seen on this or other scutes. They may be the result of disease or even post-mortem scavenging by invertebrates.

NMMNH P-39184 is an elongate (~ 93 mm long) scute fragment with a modest spike (< 20 mm tall) emanating from near the posterior edge (Fig. 8D). This is probably a caudal lateral, or, possibly, distal caudal paramedian scute. It retains the strongly radial pattern of pits, grooves, and elongate ridges.

NMMNH P-33101 is a large right(?) lateral cervical scute with a massive (137 mm long) spike emanating from the approximate center of the scute (Fig. 8G). Although we interpret this as a right cervical lateral scute, with a posteriorly recurved spike, there is no obvious anterior lamina. However, as we interpret the specimen, the medial flange would be shorter, the lateral flange wider, and the spike posteriorly recurved. Furthermore, the medial margin of the scute is thus thickened for articulation with the corresponding paramedian scute.

One of the original paratypes, NMMNH P-29045, is an incomplete right? cervical scute, and one of the original specimens Snyder discovered at the quarry (Fig. 8B). It is just a fragment of the spike of a right(?) lateral scute, but is ovoid in cross-section and the original basis for identifying *Dsmatosuchus* at the quarry (e.g., Heckert et al., 2000). Its shape most closely resembles a fourth cervical lateral scute of *D. haplocerus*, but we are not sure exactly where it may have come from on the spikier *D. chamaensis*, other than to note that it is likely a cervical lateral scute. The preserved portion of the spike measures 64 mm in length. The scute is broken anteriorly and posteriorly, and measures approximately 29 mm tall. The spike is oval in cross-section. There is a small foramen on the internal surface corresponding to the spike.

Recently prepared material reveals a new morphology of aetosaur scute that we report here and tentatively assign to *D. chamaensis*. Unfortunately, most of the scutes are poorly preserved, and none are complete. The best-preserved of these scutes, NMMNH P-35993 (Fig. 8A), is a strongly compressed, slightly recurved, lateral spike with little of the medial or lateral flanges preserved. The presumed posterior margin is strongly emarginated, and the remnants of the flanges meet at a strongly acute (< 45°) angle. A similar specimen (NMMH P-32794) has a nearly complete dorsal(?) flange that is beveled (concave medially) to articulate with a complex paramedian scute. It, too, has a strongly acute angle of juncture between the lateral and dorsal flanges. NMMNH P-37305 appears similar, but is even less complete.

One of the original paratypes, NMMNH P-33100, is generally

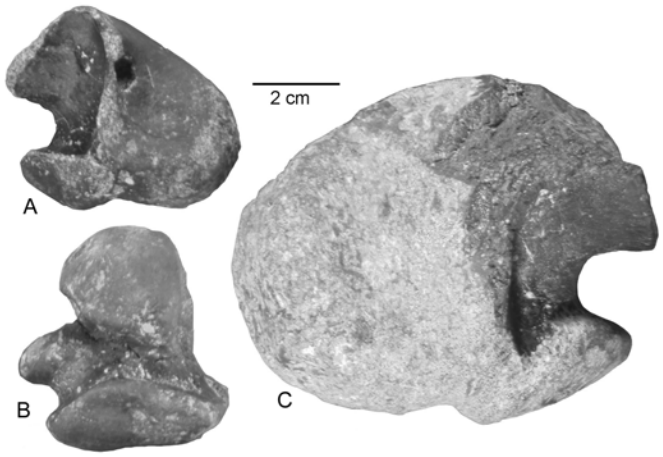

FIGURE 9. Tarsals of *Desmatosuchus* from the Snyder quarry. **A**, left astragalus, NMMNH P-33927, in posterior view; **B**, right calcaenum, NMMNH P-33931, in dorsal view; **C**, right astragalus, NMMNH P-33932, in posterior view.

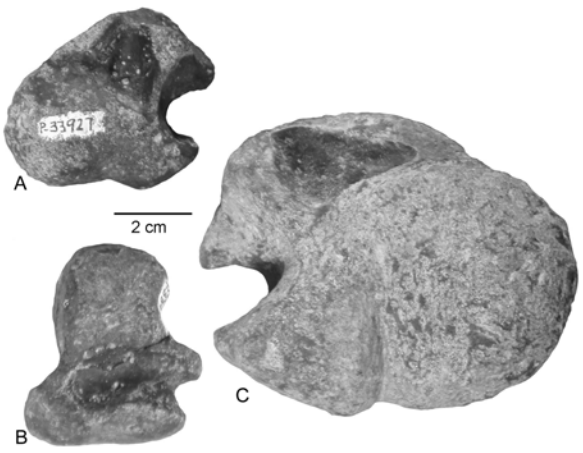

FIGURE 10. Tarsals of *Desmatosuchus* from the Snyder quarry. **A**, left astragalus, NMMNH P-33927, in anterior view; **B**, right calcaenum, NMMNH P-33931, in ventral view; **C**, right astragalus, NMMNH P-33932, in anterior view.

similar to this morphology (Fig. 6K-L). We (Zeigler et al., 2002a) originally interpreted this scute fragment as a third lateral cervical spike missing the scute body and the tip of the spike (Figs. 6K-L). The horn is 73 mm long, minus the tip, and is smooth, although the base is quite rugose. Very faint grooves are present along the dorsal and ventral sides of the spike. The bone surface itself is in poor shape and flakes off easily, obscuring surficial morphology. The principal difference between this scute and the specimens described in the previous paragraph is that the spike in NMMNH P-33100 is generally oval in cross-section.

Overall, these three scutes do not closely resemble any other scutes of *D. chamaensis* from the Snyder quarry, nor do they at all resemble known specimens of *Typothorax*. The most closely resemble UMMP (University of Michigan Museum of Paleontology) 8869, a left cervical(?) lateral scute that Lucas et al. (1995) tentatively assigned to *Paratypothorax*. Presently, we are re-studying the *Paratypothorax* specimens described by Hunt and Lucas (1992), and there are some strong similarities between these specimens corresponding to the shape of the minimal dorsal flange. However, given the absolute lack of *Paratypothorax* dorsal paramedian scutes (which are readily distinctive) from the Snyder quarry, we are hesitant to assign these scutes to that taxon.

Appendicular elements

The best preserved appendicular elements of *Desmatosuchus chamaensis* from the Snyder quarry are a right calcaneum (NMMNH P-33931; Fig. 9B, 10B), a very large right astragalus (NMMNH P-33932; Fig. 9C, 10C), and a smaller left astragalus (NMMNH P-33927; Fig. 9A, 10A). The calcaneum is a moderately robust bone that is not as dorsoventrally compressed as the calcaneum of *T. coccinarum*. The specimen is 50 mm from proximal to distal surface, 29 mm across the distal surface, 41 mm across the proximal surface, and 39 mm across the fibular facet. On the ventral aspect, the proximal end is a strongly developed lip that projects dorsally and slighty distally. Anterior of this ridge is a moderately deep and narrow convexity that runs lateral to medial. It wraps down onto the proximal side of the medial projection and provides the articular point for the distal end of the fibula. Anterior of the fibular facet is a gently convex surface that is approximately 2/3 of the bone's length. On the dorsal aspect, the proximal end is similar to the ventral aspect. Anterior of the proximal ridge is a deep constriction running mediolaterally that is subdivided by two gentle ridges that run proximal-distally. The distal 2/3 of the bone is a strongly bulbous surface that is much more convex than the equivalent surface of the ventral aspect. On the medial aspect, the proximal end is once again a strong ridge that develops from the proximal surface itself. A short constriction sits anterior to the ridge that flares medially into a concave projection that is perpendicular to the body of the calcaneum. The projection is then followed distally by a deep, round concavity that then rises medially up into the bulbous distal end. The lateral aspect shows a moderately developed lip on the proximal end, but the majority of the surface is a gentle concavity that seats part of the distal fibula. This calcaneum is nearly identical to that illustrated by Long and Murry (1995).

The two astragali are quite similar in all features, apart from the large size of the right astragalus. Here, we describe the left astragalus as it is more complete than the larger right astragalus. The astragalus is a trapezoidal bone that is moderately robust in the smaller specimen and extremely robust in the larger. The ventral aspect is a single, mostly smooth articular surface consisting of two convexities that are separated by a narrow, gentle trough. The dorsal aspect consists of two facets: a lateral facet that is laterally angled to accept part of the distal fibula and a medial facet that sweeps medially, then posteroventrally along the posterior aspect, to accept the distal end of the tibia. The posterior aspect has a moderately deep concavity on the lateral side that sweeps down from ventral and lateral up along the midline to the dorsal aspect. A prominent, thin ridge runs dorsoventrally up the middle of the posterior aspect. This ridge curves very slightly, such that it is gently concave towards the lateral aspect. A deep, subround pit lies immediately medial to the midline ridge in the upper half of the posterior face. The medial half of the posterior aspect is gently concave ventrally, then sweeps up to become gently convex dorsally and laterally, forming part of the articular surface for the distal tibia. The anterior aspect has a quite bulbous ventral half that becomes very slightly concave on the medial side of the face. In the middle of the anterior face is a moderately deep, subtriangular depression. The lateral margin of the anterior aspect curves up around the articular facet for the calcaneum that lies on the lateral face. The medial aspect is divided diagonally from posteroventrally to anterodorsally by a line of inflexion. Posterior and dorsal of this line is the tibial facet, which is gently concave and sweeps up to the dorsal surface along the posterior aspect. Anterior and ventral of this line is a gently convex protuberance. The lateral aspect has a bulbous projection on the ventral portion that is followed dorsally by a deep concavity that houses the "peg" of the calcaneum. The dorsal portion of the lateral aspect has a triangular projection that is directed laterally and somewhat posteriorly. Together the concavity and projection form a deep "hook."

The left astragalus is 44 mm dorsoventrally, 49 mm mediolaterally at its widest, and 41 mm across the narrowest point. It is 26 mm anteroposteriorly on the medial side and 20 mm on the lateral side. It is

also 17 mm anteroposteriorly at the dorsal end. The right astragalus is 77 mm dorsoventrally, 95 mm mediolaterally at its widest and 77 mm across the narrowest point. It is 52 mm anteroposteriorly on the medial side, 39 mm on the lateral side and 26 mm at the dorsal end. This specimen has had the midline ridge of the posterior face broken off and the pit that lies medial to the ridge is obscured by the damage.

Referred specimens

Zeigler et al. (2002a) interpreted two other specimens as scutes of *D.* chamaensis, both from the Bull Canyon Formation in east-central New Mexico. These are UCM (University of Colorado Museum, Boulder) 47725 and NMMNH P-4894, and we re-illustrate and describe them here as well (Figs. 6H-I, 6C, respectively).

We interpret UCM-47725 as a right paramedian scute (Fig. 6I), in excellent condition, with a sharply recurved spike (Fig. 6H). This spike is slightly shorter than that of NMMNH P-32795. The irregular ridge and groove pattern is less distinct than NMMNH P-32795, but is still apparent. The scute is 97 mm long and 85 mm wide with a 95 mm-long recurved spike with an essentially flat base. The spike is smooth in the basal region with foramina developing towards the tip and circular in cross-section. The ventral surface is smooth, lacks a ventral keel, and has a faint depression below the spike. Parrish and Carpenter's (1986, fig. 11.3) drawing of this scute misrepresents the degree of curvature of the spike and its size relative to the scute body.

NMMNH P-4894 is a portion of a recurved spike from a paramedian scute (Fig. 6C). The spike has a ridge along the anterior side, creating an oval to triangular cross-section. This fragment is 55 mm long and is missing both the tip and the body of the scute. Foramina become more common towards the tip, though the tip itself is missing.

DISCUSSION

Typothorax coccinarum is the most common Revueltian aetosaur in the Chama basin and throughout the American West. Indeed, the type specimen of *T. coccinarum* was collected by E.D. Cope near Gallina on the western edge of the Chama basin (Lucas and Hunt, 1992; Hunt and Lucas, 1993; Heckert and Lucas, 2002a). Additionally, the nearby Canjilon quarry yields several specimens of *T. coccinarum* (Long and Murry, 1995; Martz, 2002). Indeed, aside from the nearly complete specimen illustrated by Hunt et al. (1993), the Canjilon and Snyder quarries are the only localities that yield associated to articulated *Typothorax* fossils. Like the Canjilon quarry, the Snyder quarry sample of *Typothorax* is important in that it provides unambiguous evidence of the co-occurrence of *Pseudopalatus* and *T. coccinarum.*

Given the great differences between *D. chamaensis* and all other aetosaurs, as well as the significant disparity in paramedian scute morphology between *D. chamaensis* and *D. haplocerus*, it is worth addressing the question of why *D. chamaensis* is not a distinct genus. We (including Zeigler et al., 2002a) note that in spite of the unique morphology of the spikes on some paramedian scutes of *D. chamaensis*, key features of *D. chamaensis* are also synapomorphies of *Desmatosuchus* generally (Heckert and Lucas, 2000). These include the presence of anterior laminae on both paramedian and lateral scutes, and large recurved spikes on the lateral scutes. Other typical *Desmatosuchus* features are also present, including the relatively irregular size and shape of pits on the dorsal paramedian scutes and the low boss just medial to the center of the scute, even if these traits are of uncertain polarity. Indeed, the only diagnostic feature of *D. haplocerus* scutes we have not observed in *D. chamaensis* are the relatively long, narrow, and thick cervical paramedian scutes with "tongue-and-groove" (interdigitating) articulations on their lateral and medial margins. Therefore, we interpret *D. chamaensis* as a more autapomorphic species of *Desmatosuchus* than *D. haplocerus*, and see no need to erect a new genus for this taxon.

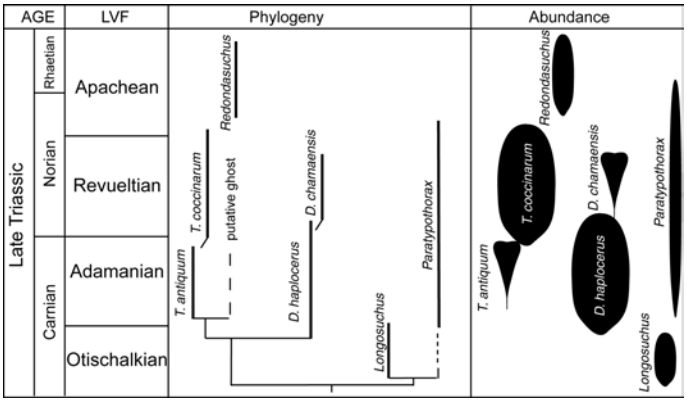

FIGURE 11. Biochronology, phylogeny, and apparent abundance of the species of *Desmatosuchus* and *Typothorax* during the Late Triassic.

Similarly, *T. coccinarum* is clearly a more derived aetosaur relative to *T. antiquum*. As enumerated by Lucas et al. (2002), the principal differences between the two taxa lie in the size and shape of the paramedian scutes, as well as some differences in the ilium. Specifically, the paramedian scutes of *T. antiquum* are much less wide, with coarser and denser pitting than those of *T. coccinarum*. The lateral scutes of the former also have more pronounced grooves, and the ilium is much more robust with a more prominent and thicker peduncles, lateral buttress, and iliac blade. Although Lucas et al. (2002) did not run a phylogenetics analysis, it is obvious that *T. antiquum* is much more primitive than *T. coccinarum*. Therefore, as Lucas et al. (2002) demonstrated, the most parsimonious phylogenetic explanation of the two species is that the older and more primitive *T. antiquum* evolved into the more derived *T. coccinarum* (Fig. 11). This is, we believe, an exceptional record of anagenetic evolution in a lineage of fossil archosaurs.

Zeigler et al. (2002a) documented a similar change in *Desmatosuchus*. *D. haplocerus* is an autapomorphic taxon by any analysis (e.g., Parrish, 1994; Heckert and Lucas, 1999, 2000). However, it is clear that *D. chamaensis* is much more so, yet clearly retains many characteristics that are typical of *D. haplocerus*.

It is interesting that the two genera, *Typothorax* and *Desmatosuchus*, appear to have inverse relationships in terms of abundance through time (Fig. 11). In strata of Adamanian age, *D. haplocerus* is particularly common, and more common than the Adamanian index taxon *Stagonolepis* (Long and Ballew, 1985; Long and Murry, 1995). The coeval *T. antiquum*, however, is exceptionally rare, known only from the type and a few referred specimens (Lucas et al., 2002a). In contrast, *T. coccinarum* was, until recently, the only recognized mid-late Revueltian aetosaur in the Chinle Group (Long and Murry, 1995), and remains far more common than other taxa, which are known to include *Paratypothorax* and *Aetosaurus* (Heckert and Lucas, 1998; Small, 1998) as well as *D. chamaensis*. Some time early in the Revueltian, there is an overlap of stratigraphic ranges of *D. haplocerus*, *D. chamaensis*, *T. coccinarum*, and some other taxa (Fig. 11). Still, separate biochrons for both species of both *Typothorax* and *Desmatosuchus* are identifiable, and the overlap of these biochrons must represent an exceedingly brief period of time.

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